A comparison of the meiotic prophases

IN

ŒNOTHERA LAMARCKIANA and ŒNOTHERA HOOKERI

BY

T. ELLIOT WEIER

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan.

(Reprinted from « La Cellule », *vol. XXXIX, fascicule 3, 1930)*

(Memoir received November 20, 1929)

LIERRE
Typ. de JOSEPH VAN IN & Cie
Grand'place, 38

LOUVAIN
A. UYSTPRUYST, Libraire
rue de la Monnaie

LA CELLULE

Recueil de travaux originaux de Cytologie, de Biologie et d'Histologie générale.

Cette Revue paraît par fascicules d'importance variable. Deux à quatre fascicules constituent un tome — généralement annuel — de 450 pages in 4°, avec 20-35 planches en double page (noires ou en couleurs) et des figures dans le texte.

Le prix de l'abonnement est rétabli au taux de 1914 : **50** francs-or = **10** $ = **2** £, ce montant comportant les frais d'envoi. Il est abaissé à **6** $ pour les pays à change déprécié (France, Italie, Pologne, Roumanie, Yougoslavie, Tchécoslovaquie) et à **175** fr. *belges* (**5** $) pour la Belgique. Pour les libraires, ces réductions sont subordonnées à la désignation des destinataires.

Les abonnements sont reçus par l'Éditeur : **A. UYSTPRUYST, Librairie Universitaire, rue de la Monnaie, Louvain.**

* * *

Les auteurs sont priés de n'envoyer que des mémoires *dactylographiés* ou, au moins, très lisiblement écrits. Les dessins destinés à être reproduits *sur planches* seront faits à l'encre de chine ou au crayon-carbone et accompagnés d'un calque indiquant leurs positions respectives (justification : 31 × 22 cm. pour les planches en double page; 15 × 22 cm. pour les planches simples). Les dessins destinés à figurer *dans le texte* seront faits, de préférence, *au trait*.

Cinquante exemplaires de leurs travaux sont remis gratuitement aux auteurs. Des exemplaires supplémentaires sont fournis au prix coûtant.

Les manuscrits et toute demande concernant *la Rédaction et les Échanges* doivent être adressés à **Mr P. MARTENS, professeur à l'Université, rue Marie-Thérèse, 23, Louvain.**

Les directeurs :

G. GILSON & V. GRÉGOIRE

PROFESSEURS A L'UNIVERSITÉ DE LOUVAIN.

Sommaire du fascicule 3 :

T. ELLIOT WEIER (Ann Arbor, U. S. A.) : A comparison of the meiotic prophases in *Œnothera Lamarckiana* and *Œnothera Hookeri* (2 plates).

J. KOERPERICH (Louvain) : Étude comparée du noyau et de la cinèse dans *Nothoscordum*, *Beschorneria* et *Eucomis*; relations morphologiques entre noyau et protoplasme (4 planches).

V. JUNGERS (Louvain) : Recherches sur les plasmodesmes chez les végétaux (4 planches).

A comparison of the meiotic prophases

IN

ŒNOTHERA LAMARCKIANA and ŒNOTHERA HOOKERI

BY

T. ELLIOT WEIER

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan.

(Reprinted from « La Cellule », *vol. XXXIX, fascicule 3, 1930)*

(Memoir received November 20, 1929)

LIERRE
Typ. de JOSEPH VAN IN & Cie
Grand'place, 38

LOUVAIN
A. UYSTPRUYST, Libraire
rue de la Monnaie

R. UNIV.
BIBLIOTHEEK
LEIDEN

A comparison of the meiotic prophases

IN

ŒNOTHERA LAMARCKIANA and ŒNOTHERA HOOKERI (1).

INTRODUCTION.

There is a long history from REMAK's simple account in 1841 of the division of the red blood corpuscle to the chromosome pictures of MC CLUNG (1927, 1928) and SHARP (1920) and the chromosome maps of MORGAN (1926). It was forty years after REMAK described his simple scheme before FLEMMING and STRASBURGER established the fact that cell division is marked by a breaking up of nuclear substance into chromosomes which split lengthwise during mitosis. The major problems then became associated with the behavior of these bodies at maturation. The brilliant minds of ROUX and WEISMANN recognized the importance of a reduction division described in *Ascaris* by VAN BENEDEN (1883), and established for plants by STRASBURGER (1888). The next period is marked by the controversies over the behavior of the chromosomes during the reduction division. The work of the SCHREINERS, GELEI, ALLEN, JANSSENS, WILSON, MC CLUNG, GRÉGOIRE and many others have definitely shown that the peculiarities of the reduction lie in a side-by-side pairing of two homologous somatic chromosomes.

The history of this cytological development has been paralleled by an equally remarkable period in the growth of genetics roughly marked by the demonstration of parallelism between Mendelian segregation and chromosome behavior, the evidence for gene mutations, linkage and crossing-over. With the exception of their application to Œnothera these principles are

(1) Papers from the Department of Botany of the University of Michigan, Ann Arbor, U. S. A., n° 316.

generally accepted. A form of linkage is present in Œnothera, but Mendelian inheritance and the independent segregation of chromosomes are known in only a few species, while crossing-over and the presence of gene mutations have yet to be clearly demonstrated. In addition to this an explanation which will be generally acceptable is desired for a number of peculiarities of breeding (SHULL, 1928).

The development of the chromosomes during their meiotic history is as exceptional in Œnothera as is the genetical behavior of this genus. GEERTS (1907, 1908), GATES (1908), and DAVIS (1910, 1911) were the first to point out the pecularities of meiosis. They observed no parallel threads during the prophases. The stage of synizesis was marked by an extreme contraction of the chromatic material. The second contraction figure consisted of another much contracted mass of chromatin. Diakinesis was marked, not by pairing chromosomes, but by chains and odd chromosomes scattered throughout the nucleus. No pairing was present at metaphase of the heterotypic division while the chromosomes drew away from each other very irregularly at anaphase. CLELAND (1922, 1923) has shown that these irregularities in the later stages of meiosis were really the formation of chains of chromosomes peculiar to certain forms all of which appear to be heterogametic species. Since there is apparently such profound lack of homology between the chromosome sets, BARTLETT (1915) and BLANCHARD (1929) have preferred to call such species heterogametic instead of heterozygous, the latter term generally implying only allelomorphic contrasts. In the homozygous *O. franciscana*, CLELAND (1922, 1927) found no chains but instead an independent segregation of chromosomes, as had been described by DAVIS (1909) for another homozygous species, *O. grandiflora*. Although CLELAND has not succeeded in presenting a logical system of development from the earlier prophases, he postulates telosynapsis as the mode of chromosome pairing. This conclusion was drawn mainly from the arrangement of the chromosomes at diakinesis. He, however, pointed out (CLELAND 1922) that the prophases of Œnothera bear no resemblance to the mode of chromosome pairing described by FARMER and MOORE (1905).

EMERSON (1924), OELKERS (1926), HÅKANSSON (1926, 1928), VALCANOVER (1926), KIHARA (1927), SINOTO (1927), SHEFFIELD (1927), SCHWEMMLE (1927) and KULKARNI (1929) have fully corroborated CLELAND's descriptions of chains of chromosomes in heterozygous material at the stage of diakinesis. All agree that, at metaphase of the heterotypic division, chromosomes are in

a zig-zag arrangement. VALCANOVER (1926) describes a type of pairing as taking place after a zig-zag period. There can be no doubt of the actual existence of the chain and zig-zag arrangement of the chromosomes at diakinesis and in the following metaphase. It seems certain that the various configurations are constant for each species.

BOEDIJN (1924, 1925) and LELIVELD (1928) are of the opinion that the chromosomes pair by twos and that no chains exist. The former author claims to have found seven pairs of chromosomes in *O Lamarckiana* at the period of diakinesis but other workers (CLELAND and HÅKANSSON) found a chain of twelve chromosomes together with one pair. LELIVELD while agreeing with BOEDIJN's contention that parasynapsis takes place in *O. Lamarckiana*, does not support his observations of seven paired chromosomes at diakinesis. She claims that in place of the chain structure there takes place at this period only a chance adhesion of the chromosomes. The technique of LELIVELD is open to criticism since she used in fixation a mixture which in my experience gives extreme shrinkage of the cytoplasm and breaks up the chromosome arrangements. It is hardly possible that the chain formation reported by others after various methods of fixation and for a number of species should be an artifact, while the few fixations of LELIVELD's should alone produce the true picture of the cell, particularly when the chain structure could be more easily ruptured by harsh treatment than created by any kind of technique. I have obtained the chain arrangement in *O. Lamarckiana* with a large variety of killing solutions and am fully convinced of its presence.

STOMPS (1910), SCHWEMMLE (1926) and KIHARA (1927) working on other material and arguing from analogy have claimed that parasynapsis is the mode of chromosome association in Œnothera. KIHARA's text figures and explanations of the chromosomes in chains can be made to conform equally well to the telosynaptic interpretation. DARLINGTON (1929) in a theoretical discussion expresses the belief that parasynapsis takes place.

Although both modes of synapsis are claimed in species of Œnothera no detailed study of the synaptic stages has been made. Accounts of meiosis usually pass quickly from the archesporium to synizesis. This latter stage has been described as a dense mass of deeply staining material in which it is impossible to discern any system. The open spireme and second contraction figures, although less confusing than the previous stage of development, still await carefull study in order to determine accurately chromosome

development. The interpretation of telosynapsis has been drawn chiefly from the condition of nuclear material at diakinesis. Synapsis does not take place at this stage in either animals or plants and there is no evidence that it occurs at this period in Œnothera. It is not possible to deduce convincingly the behavior of the chromosomes at an unobserved period of development from their condition at a known meiotic stage. VALCANOVER (1926) has described pairing as occuring at metaphase, but neither his figures nor his arguments are adequate.

SHULL (1914) has expressed the opinion that a unique mode of chromosome segregation must be present to explain the genetical behavior of the Œnothera group. The hypothesis of non-homologous chromosomes (BARTLETT 1915, 1916, COBB and BARTLETT 1919, RENNER 1917) offers an acceptable interpretation, at least from a cytological point of view. Furthermore it is the species with the chains of chromosomes that show the breeding peculiarities of Œnothera, while the few species with paired chromosomes behave more normally. This matter will be treated in some detail in the » Discussion «.

It follows then, that the manner of chromosome association in Œnothera is a subject of dispute, due mainly to the confused picture presented by the killing fluids commonly used. There are present in some species chromosomes in sausage-like chains, which in contrast to paired chromosomes may be described as non-homologous. And lastly, the genetical behavior of the species having chains of non-homologous chromosomes, is strikingly different from the behavior of species with paired homologous chromosomes.

This study was undertaken in the hope of finding a killing fluid that would make possible the determination of the mode of chromosome pairing in a homozygous species and give further information on the development of the chains of non-homologous chromosomes in heterogametic species, and determine whether the meiotic behavior of the non-homologous and homologous chromosomes is associated with the genetical peculiarities present in the species concerned. For these reasons, *O. Hookeri* and *O. Lamarckiana* were the species chosen for the investigation. In the homozygous *O. Hookeri*, all chromosomes show perfect pairing while a closed chain of twelve non-homologous chromosomes is present at diakinesis in the heterogametic *O. Lamarckiana*.

For kindly criticism, I am greatly indebted to Dr. B. M. DAVIS, under

whose direction this investigation was developed. To Professor H. H. Bartlett, Dr. E. G. Anderson and Dr. S. H. Emerson, I wish to express my appreciation for the interest they have shown throughout the work. To Katherine S. Weier, I am indebted for much technical assistance concerned with the large collections made during the summer of 1928.

MATERIAL AND METHODS.

The most significant cytological studies on Œnothera have been concerned with the later meiotic stages. The early periods of meiosis have not been treated in detail. The stage called synizesis in particular is not understood because the chromatic structure is hidden in a heavily staining contracted knot. Cleland (1922) and Carrothers (1926) have suggested that this condition is an artifact produced by the killing solutions used.

To test this possibility, fixations of *O. Hookeri* and *O. Lamarckiana* were made at the Botanical Gardens of the University of Michigan in the following standard solutions, as given in Lee's »Vade Mecum«, and modifications of them : strong Flemming, Lindsay Johnson, Hermann, Allen's modification of Bouin, Gilson, Tellyesniczky, acetic-alcohol, Mann Kopsch, Merkel and a mixture of acetic and osmic acids. It was found that the material killed in the acetic-alcohol mixtures did not present the chromatic structure at synizesis in so great a degree of contraction as is usually described and figured for Œnothera material. Therefore, in the summer of 1928, extensive collections were made in a large number of killing solutions based on acetic acid and alcohol. From among these, anthers were prepared for study after fixation in the following mixtures :

A. Acetic acid	Absolute alcohol
1 part	2 parts
1 part	3 parts
1 part	4 parts
1 part	6 parts

B. Acetic acid	95 % alcohol
1 part	3 parts
1 part	3 parts of a saturated solution of picric acid in 95 % alcohol
1 part formol	5 parts acetic acid 15 parts saturated solution of picric acid in 95 % alcohol.

It is difficult to say which of these solutions gave the best results as different details were brought more into prominence according to the solution used and much depended on good fortune in staining.

All of the mixtures of the aqueous solutions caused the usual strong contraction of the chromatic material at synizesis. This stage in the acetic-alcohol fluids was always present as a ball of fine threads winding in a confused mass through the nucleus, even though somewhat contracted. This thread system was very confusing when viewed as a whole, but when thin sections were used for study a definite system of thread arrangement could be found. Often the filaments were so granular that detailed study was impossible, but in general for the study of the early prophase stages, the material fixed in the acetic-alcohol fluids was greatly superior to any fixed in the aqueous mixtures.

It seems probable that the different results obtained with the two types of killing fluids are due mainly to the waxy covering on the outer surface of the anthers, causing a slow penetration of the aqueous fluids, rather than to a direct effect of the killing mixtures upon the chromatin. The acetic-alcohol solutions are apparently not held back by the waxy layer and penetration is consequently much more rapid.

The less rapid penetration of the aqueous mixtures will naturally kill the cells more slowly. This process may be accompanied by a lowering of the surface tension of the chromatic material or a change in it from a gel to a sol state. In either case it would tend to flow together. Thus the fixed picture of the cell killed in the aqueous fluids is rather that of a pathological condition due to a slow death.

A large number of stains were tried but the short method of staining in HEIDENHAIN'S iron-alum haematoxylin proved to be the best for all material. Before staining it was necessary to mordant sections of material from acetic-alcohol mixtures over night in TELLYESNICZKY'S killing fluid.

DESCRIPTION OF MEIOTIC PROPHASES IN ŒNOTHERA HOOKERI.

A. Chromatic bodies.

In the youngest anthers the prophase chromosomes may be observed stretched across the nuclear cavity as slightly bent rods, FIG. 1. They are larger than the somatic chromosomes that may be observed in nearby cells.

As preparation for meiosis proceeds, nuclei are observed which contain chromatic bodies, FIGS. 2-3, in numbers ranging from one to twenty. Their size varies from about one half the length of the original chromosome to very small granules. These portions of chromosomes gradually disappear and a very fine system of threads becomes evident within the nucleus, FIG. 3. The sequence of stages during this short period of development indicates that chromosomes occasionally fragment after telophase following the last somatic mitosis. The chromatin in these fragments then gradually spins out into a very fine thread. There is no reason to assume that the thread formed from one chromosome becomes attached in any way to threads in the process of formation from other chromosomes.

B. Delicate thread system.

With the disappearance of the chromatic bodies a definite stage of fine threads appears, FIG. 3, which in Œnothera has always been described as a reticulum. It must, however, be noted that even with the best of lenses these threads are too delicate to determine whether or not there are actual connections between crossing threads. Anthers containing this stage of meiosis were not numerous, which would indicate that it is not a period of long duration.

So far the developments in *O. Hookeri* and *O. Lamarckiana* are very similar (compare FIGS. 1, 2, 3 with FIGS. 26, 27, 28) but following this stage the respective histories diverge.

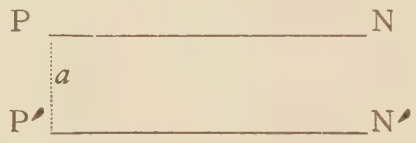
C. Leptonema.

The staining capacity of the thread system gradually increases. It is often possible to trace the threads for some distance, FIG. 4-5. Chromatic granules begin to appear more or less profusely depending upon the killing fluid used. Numerous unsuccessful attempts were made to trace accurately the entire thread system of a nucleus at this period. Nevertheless the fact was impressed upon me that a system of separate threads, and not a reticulum, exists in the nucleus at this stage of meiosis.

The chromatic granules are small and vary greatly in shape, FIGS. 4-5. They appear much more numerous in material fixed in aqueous solutions as illustrated by FIG. 4, and probably do not present a wholly true picture of the nucleus. They are less numerous after fixation in acetic-alcohol, FIG. 5.

Parallel threads are present, FIGS. 4-5, their number and length varying greatly in different nuclei. Commonly they may be observed emerging from chromatic granules, FIGS. 4-5. CLELAND (1922, p. 393) has described this condition in *Œnothera franciscana* as a resting stage »sufficiently different, however, from the typical resting condition to be noticeable and to indicate that the nucleus is approaching prophase«. He believes the parallelism to be merely chance associations of threads.

Let us consider the mathematical possibilities of two threads, each one micron in length, becoming parallel. We shall allow in this problem the relatively large deviation of one-tenth of a micron from true parallelism. PN and P′N′ are given each one micron in length. PN is fixed in space. Point P′ on line P′N′ is fixed at a given distance *a* from P. Point N′ is not fixed so that the line P′N′ may move in any direction in space. It will then become the radius of a sphere whose surface will be equal to



12.56 square microns if P′N′ equals one micron.

We have allowed a variation of one-tenth of a micron in the chance formation of parallel lines. P′N′ is fixed at a length of one micron. The variations in position of point N′ would lie in a circle whose radius is 0.05 microns. The area of this circle would be 0.0075 square microns.

The area of the surface of the sphere generated by the radius P′N′ is about 12 square microns. The area of the circle on its surface is 0.0075 square microns. There will be contained in the larger area approximately 1,600 smaller circles. So the mathematical probabilities of the chance formation of threads 1 *u* in length being parallel within one-tenth of a micron is 1 in 1,600.

If we make the length of the lines 4 microns, instead of 1, the relation between the area of the surface of the sphere and the area of the circle becomes 0.0075 to 192 giving 1 chance in 25,000 for the parallel arrangement.

It should be remembered that the delicate parallel threads must be close to a horizontal plane to be easily observed. This means that numerous cases of parallelisms are completely missed. Also the side-by-side approximations are undoubtedly progressive. It is most unlikely that the observed parallel threads in *O. Hookeri* are only chance associations for in

O. Lamarckiana, a species possessing only one pair of homologous chromosomes, parallel threads are almost entirely lacking at this stage. The attraction of the homologous chromosomes for each other would seem to be the major cause.

So far the threads have been distributed fairly evenly throughout the nucleus. They are relatively short and well separated from one another, FIG. 4-5, and the total amount of chromatic material in the threads appears small. The later period of leptonema is marked by a great change, the nucleus now passing into a condition in which the chromation, in the form of extremely fine threads, winds in a loose ball nearly filling the nucleus, FIG. 6.

The chromatic threads have apparently greatly lengthened, and have possibly become somewhat more delicate. The total mass of chromatin in the threads has increased. A comparison of FIGS. 5 and 6 will give some idea of this change. It takes place quickly as indicated by stages in cells of the same pollen sac. In material fixed in mixtures of acetic-alcohol, I find no evidence, as believed by CLELAND (1922), suggesting the flowing of chromatin material from one thread into another. The threads are still of the same diameter and it is not until later that they differ in thickness.

As has been stated before, the aqueous killing fluids, such as FLEMMING, ALLEN'S modification of BOUIN, and TELLYESNICZKY, tend to cause a coagulation of the chromatic filaments. Possibly it is this fact that led CLELAND to believe that the chromatin of one thread passes into that of another.

I was not able to observe any system in the maze of extremely fine threads which wind at this period in every direction through the nucleus.

D. Synizesis.

The term synizesis has been applied in Œenothera cytology to that strongly contracted leptotene thread system appearing as a uniform mass of chromatin with a few outlying loops. Such figures have been shown quite generally, as in the papers of GATES, DAVIS, SCHWEMMLE, SHEFFIELD, SINOTO, HÅKANSSON and others. CLELAND'S (1922) description of the stage in *Œenothera franciscana* is that of a densely staining knot with a reticular network around its periphery. BOEDIJN (1925), LELIVELD (1928), HÅKANSSON (1928), and SINOTO (1927) have shown that sufficient destaining brings out denser bodies within the knot. BOEDIJN and LELIVELD have called these

bodies » zygosomes « and have claimed that in *O. Lamarckiana* they are constantly seven in number. HÅKANSSON's (1928), SINOTO's (1927), and my own observations on material killed in the aqueous mixtures, do not agree with the report of seven constant bodies for Œnotherae possessing a chain of chromosomes. VALCANOVER (1926), although not actually observing zygosomes, assumes that they exist and makes use of them in his theory of pairing.

What is often considered as a synizesis in descriptions of meiosis in other plants and animals is not strictly comparable to the even coagulum present in preparations of Œnotherae because it has been described as a mass of threads winding more or less tightly in a ball. MEVES, JANSSENS, MC CLUNG, the SCHREINERS and others believe that the synizesis figure is an artifact. TAYLOR (1922) reports that proper fixation does not give the contraction of chromatin in Gasteria. CARROTHERS (1926) is critical of the figure as described in Œnothera, believing it to be due to the killing fluids, while CLELAND (1922) strongly suggests that such may be the case. Synizesis has been described in the living cell, although, in view of the difficulties, such studies should be carried out with greater care and detail than has so far been presented.

As stated, it was mainly with the study of this period in mind that the large number of killing fluids was tested. A comparison of FIGS. **6** and **7** will give some idea of the divergent results obtained. FIG. **7** is from material fixed in strong FLEMMING, which is an aqueous fluid. It produces a heavy coagulum of chromatin. On the other hand, the quickly penetrating acetic-alcohol combinations give a definite system of threads, FIG. **6**, which form a loose ball nearly filling the nucleus. In thick sections of the acetic-alcohol material the confusion is great and is further enhanced by the granular condition and length of the threads.

It is of course necessary to have some criterion for judging just which of these conditions actually is the normal one. We have on the one hand a heavy, dark, evenly staining mass of chromatin, on the other a system of threads. There can be no doubt that a coagulum could be produced from a system of threads by imperfect fixation. On the other hand it is difficult to concieve of a killing fluid that would form a delicate system of chromatic threads out of a formless mass of nuclear material. It follows from this that the normal living chromatic structure of the nucleus is much more likely to be in the form of threads, than it is to be a heavily staining mass. For

these reasons, the zygosomes of Boedijn (1924) and Leliveld (1928) are considered to be artifacts, and synizesis to be a greatly contracted condition of the nucleus during the zygotene period of meiosis.

E. Zygonema.

The thread system of chromatic material at the end of the leptotene period of meiosis is extremely delicate and quite uniform, fig. 6. It is arranged in a loose ball that nearly fills the interior of the nucleus and presents a picture of apparent confusion. The condition is not one of long duration.

The next stage is marked by slightly thicker threads and somewhat less confusion in the appearance of the chromatic material. Sections of nuclei were used for most of the studies upon this stage. Parallel threads are frequently present and often united over considerable lengths, figs. 8*b*, *c*, *d*, 9, 10*a*. Threads which twist about one another are also in evidence, figs. 8*a*, 9*a*, 10*b* and *c*. Single threads are still present and it is sometimes possible to recognize certain of them as thicker than others, fig. 9. Corresponding granules occasionally occur on some of the parallel filaments, fig. 10*b*.

The condition of the nucleus is very suggestive of a zygotene stage of development, caused by the progressive side-by-side pairing of homologous chromosome filaments. No nuclei were observed in which all of the threads were parallel or twisted about each other as has been reported for other material. This is possible because the association is progressive, and the components cannot be distinguished after the threads have become bivalent.

It must be admitted that material of Œnothera, even after fixation in acetic-alcohol mixtures, presents peculiar difficulties for the study of this period of meiosis. The granular structure of the chromatin, which appears after fixation, often makes clear understanding impossible and the tortuous character of the threads adds further to the confusion. However, a definite parallelism, twisting or union of some of the filaments may be observed in almost every case where it is possible to make a careful study of the nucleus. The evidence seems to indicate a side-by-side association of the chromatic threads representing chromosomes.

As zygonema progresses in *O. Hookeri* the threads become thicker, fig. 11, and they stain more deeply. Some contraction does occur which draws the chromatin away from the nuclear membrane. The complicated

loose ball of chromatic threads present in the late leptonema changes gradually, through a process of shortening and thickening, to a condition in which the individual threads may readily be traced for considerable lengths. There are then two definite movements of chromatic material taking place during the zygotene period, 1° a progressive side-by-side pairing of the leptotene threads, and 2° the shortening and thickening of the threads to a condition in which they may be traced and counted.

F. Pachynema.

As the microsporocytes separate from one another the chromatic threads continue to shorten and thicken and take the stain well. The acetic-alcohol fixations no longer cause the formation of the granular conditions so prevalent in the earlier stages. There seems to be no doubt as to the existence of a system of separate threads. I can find no evidence of a reticular structure at this period as reported by CLELAND (1922). The threads finally reach a stage in late pachynema when the shortening and thickening has so simplified the tangle that their number and course may be followed. This period is marked after both types of fixing fluids by loops radiating from a central mass, FIGS. **12-16**. I am inclined to believe that this mass is an artifact, although the best of my material showed it.

In nuclei favorable for detailed study it is possible to trace the course of seven threads, illustrated in FIGS. **12-17**. Attention is called to FIGS. **15** and **17** which show in detail the seven threads present in FIGS. **14** and **16**, respectively. Most of these threads are loops from an irregular central mass of chromatin. A few, however, show one free end, FIGS. **12***a*, **13***a* and *d*, **14***a*, **16***a*. The shorter, heavier threads are similar to the radiating arms characteristic of second contraction, FIGS. **13***d*, **14**, **15***a* and *b*, compared with FIG. **18**, indicating that the seven long threads shorten and thicken until they finally produce seven arms extending from a central coagulum.

Numbers of the threads may show a definite split to be interpreted as a separation of the leptotene threads which became associated in zygonema. In some cases the univalent threads twist about each other, FIGS. **16**, **17***b*, *c* and *d*, while in other cases they lie quite apart from one another, FIGS. **13***c*, and **15***c*. This split condition makes it quite impossible to believe that the seven threads are formed by the end to end association of the fourteen chromosomes. Seven threads or loops may be

counted in each cell shown, and a number of these are definitely double. This is good evidence that the parallel leptotene threads of earlier periods have shortened and thickened and become associated side-by-side after the manner of parasynapsis.

G. Second contraction.

The second contraction figure in *O. Hookeri* is always present and is marked by a high degree of regularity. It consists of a central mass of chromatic material with seven arms extending from it, FIG. **18**. These arms usually appear single in the earlier part of the period but a double structure becomes evident as development proceeds. There are finally seven bivalent arms which have been formed by the continued shortening and thickening of the seven bivalent threads of the previous period, FIGS. **12-17**.

There is not much difference in the appearance of the material whether fixed in solutions of acetic-alcohol or in the aqueous mixtures, but a light stain after the acetic-alcohol occasionally shows faintly the outlines of heavy chromatic threads throughout the central coagulum. It seems probable that the darkly staining shapeless mass represented in most drawings of this period is in reality an artifact due to imperfect fixation. Whatever may be the cause of the coagulum the outlines presented are most various. The arms extend in all directions. No two cells show them of the same length or shape, nor are two chromatic masses ever of the same form. Anthers in this period of meiosis generally contain the preceding stage of pachynema and the following stage of diakinesis, indicating that the phase of second contraction is not of long duration.

The contracted material now begins to break apart giving smaller masses of various sizes and of irregular forms associated with one or more of the arms, FIG. **19**. Separation continues until the arms, now bivalent, become free from one another, FIGS. **20-22**. It becomes increasingly clear, through the breaking apart of the original central mass, that the chromosomes are forming by the condensation and shortening of the bivalent pachytene threads. The time at which they may be distinguished as chromosomes varies greatly in different cells. In FIG. **23**, two arms have broken away from the coagulum and are recognizable as pairs of chromosomes. Other cells show the arms separating more uniformly. When the bivalent chromosomes first appear, they are relatively long and the univalents are tightly pressed against each other, FIGS. **20** *a*, **23** *a*. In later stages

the univalents are usually more evident. The shortening and thickening of the chromosomes and the fragmentation of the mass continues until finally the pairs become seven bivalent rings, FIGS. **24-25**. Some of them may be linked, FIG. **24**, but eventually they separate completely from one another, and are later rather evenly distributed through the nucleus, FIG. **25**.

It has thus been possible to trace, step by step, the development of the seven paired chromosomes in *O. Hookeri* from the pachytene stage of seven zygotene threads, through a gradual shortening and thickening of these threads to form the seven arms extending from the central mass peculiar to second contraction. During this period, the arms become separated by the breaking up of the chromatic coagulum, and by further condensation of the arms chromosomes arise which are characteristic of the diakinesis stage of *O. Hookeri*, FIG. **25**.

There would seen to be only one interpretation of this history as given for the prophases of meiosis in *O. Hookeri*. The development of the chromosomes follows the scheme of parasynapsis.

DESCRIPTION OF THE MEIOTIC PROPHASES IN ŒNOTHERA LAMARCKIANNA.

A. Chromatic bodies.

The appearance of the contents in the younger microsporocytes of *O. Lamarckiana* is quite the same as in *O. Hookeri*. The chromatic bodies are very conspicuous. Their number is variable, covering about the same range as those in *O. Hookeri*, from one to twenty, FIG. **27**. They are believed to arise from the chromosomes that enter the microsporocyte after the last mitosis in the archesporium, FIG. **26**. As they gradually disappear, a fine thread work takes their place in the nucleus, FIG. **28**.

B. Delicate thread system.

The period of a fine thread system is of short duration and identical in appearance with that of *O. Hookeri*. Delicate threads weave a confused arrangement resembling a network. The threads are too delicate to determine with certainty whether or not there are actual connections between them, FIG. **28**.

C. Leptonema.

Stages follow in which the chromatic threads become thicker, stain more deeply, FIG. **29**, and may be traced for short distances. They appear

quite suddenly from a confused tangle, wind in and out among other threads in the nucleus and finally disappear from view. It is quite certain that where they can be clearly observed they do not form a chromatic reticulum.

As in *O. Hookeri*, it is quite impossible to trace accurately the thread system in the whole nucleus, but in attempting to do it one becomes impressed with the probability that the threads are quite separate and distinct, FIG. **29**. There is no evidence that the chromosomes have become united in any manner.

No parallel threads were observed during leptonema as noted in *O. Hookeri* (compare FIG. **29** with FIGS. **4-5**) and the absence of parallelism at this stage of meiosis in *O. Lamarkiana* is striking. In only one nucleus have I observed two threads parallel and emerging from a chromatic granule. That case possibly presented the initial pairing of the two homologous chromosomes that are present in *O. Lamarckiana*.

The threads of the reticulum now lengthen and draw away slightly from the nuclear membrane. They are very delicate, twisting and winding in a loose ball, FIG. **30**. The confusion is so great, that it is impossible to determine any system in the arrangement.

HÅKANSSON (1926 and 1928) reports parallel threads at the early leptotene period for *O. Lamarckiana* and *O. Lamarckiana var. gigantea diploid* which also has a closed chain of chromosomes. He states, however, that „Die Paralletität war aber nicht häufig oder regelmässig genug, um als irgend eine Paarung gedeutet werden zu können". I have failed to find support for HÅKANSSON's figures, except the one case of parallelism probably associated with the two homologous chromosomes of *O. Lamarckiana* which are not in the chain of twelve. It is quite certain that *O. Hookeri* presents a much more orderly arrangement of threads as well as more parallelism than is shown in HÅKANSSON's figures for *O. Lamarckiana*.

D Synizesis.

There has been figured in all accounts of meiosis in *O. Lamarckiana* the stage of a contracted leptotene thread system called synizesis. Here as in *O. Hookeri* it seems probable that the flowing together of the chromatic material accompanied by contraction is largely, if not wholly, the result of imperfect fixation. After FLEMMING, ALLEN's modification of BOUIN, TELLYESNICZKY and other aqueous killing fluids the contraction of chromatin is

very great, so that threads and masses lie in a tight ball or knot. There is some contraction after fixation in the more rapidly penetrating acetic-alcohol mixtures, but not the formation of a coagulum. FIG. 31 shows an optical section of a nucleus after fixation in acetic-alcohol at the stage when aqueous killing fluids would present a picture of contracted chromatin material similar to FIG. 7. In this account of *O. Lamarckiana* as in *O. Hookeri*, the stage of synizesis, as usually described by Œnothera cytologists, is considered to be a greatly contracted condition of the zygotene period of meiosis.

E. Zygonema.

Parallelism of threads as noted for *O. Hookeri* is not evident in *O. Lamarckiana*. The threads at all stages are free and independent of one another as they wind about within the nucleus, FIG. 32. There is nothing of the frequent evidence of pairing present in *O. Hookeri*, as illustrated in FIGS. 8-11, which should be compared with FIGS. 31-33. In only two nuclei have I observed two threads parallel, FIG. 33. This probably shows the association of the two homologous chromosomes present in *O. Lamarkiana*. Except for this behavior which may be expected during the condensation of the pair of homologous chromosomes, independent of the closed chain of twelve, there seems to be no stage of zygonema in *O. Lamarkiana*.

During leptonema the chromatic threads elongate and become more delicate. The process is reversed at this stage and the threads gradually become shorter and thicker. Nuclei are present in which both thick and thin threads may be observed, FIG. 31. This process has been interpreted as the growth of one filament at the expense of material derived from others, but with this conclusion I cannot agree. The threads are always separate and distinct from one another after fixation in acetic-alcohol. Material does not appear to be in the process of movement from one filament into another. As pointed out before the conditions interpreted as evidence for such movement of material (CLELAND 1922) are probably the result of fixing fluids that penetrate too slowly.

F. Pachynema.

The shortening and thickening of the threads continue until the system becomes so simplified that the threads may be traced as they emerge from a central coagulum of chromatin. This coagulum is probably the result of imperfect fixation. In a number of instances thirteen threads are present,

FIGS. 34-35, and this number agrees with the twelve non-homologous chromosomes which form the closed chain plus one bivalent which results from the pairing of the two homologous chromosomes. In FIG. 34, thread *m* is probably the bivalent filament. The chromatic threads usually take the form of loops with their ends embedded in a mass in the center of the nucleus. Ends, however, are frequently seen, FIG. 34, showing clearly that a continuous spireme is not present at this period. Even were no ends present, it cannot be assumed that a continuous thread exists when so much is concealed in the central coagulum. It is under such conditions that a continuous spireme has been reported for the Œnothera group. The evidence presented here seems clearly to show that such is not the case.

G. Second contraction.

The second contraction figures in *O. Lamarckiana* are the most difficult of all stages to interpret. They present an almost endless variety of forms regardless of the fixation employed and it seems hardly possible that a true picture is presented in stained and sectioned nuclei. The chromatin may be shown as an irregular mass of heavily staining material, FIG. 36, or there may be arms extending from a central mass in numbers varying from one to as high as thirteen. This latter condition, FIGS. 37-38, was observed in only six cells. The typical picture of early second contraction figure, varied though it may be, is not that of loops radiating from a central mass. The figure is rather one of arms extending from the central chromatic coagulum, FIGS. 37-38.

Pachynema shows thirteen threads of varying lengths and diameters, FIGS. 34-35. Thirteen arms have been counted definitely in the second contraction period, although in only six nuclei. The arms are always present, however, although in varying numbers. Apparently the killing of the cell brings about such a contraction of the chromatic material that the threads are frequently completely merged in the central mass. There is a perfect sequence of stages from pachynema to the early second contraction figures and the evidence seems very clear that the arms of the latter period of meiosis have developed through shortening and thickening of the pachytene threads.

In FIGS. 37 and 38 thirteen arms are shown. Twelve of them, *a* to *l*, are single and would eventually have formed the closed chain of chromosomes present at diakinesis. The remaining arm *m* shows a split end and would probably have developed into the pair of homologous chromosomes.

The table records a count of arms observed in 78 nuclei in the stage of second contraction. In making the counts only cells containing the definite arms of second contraction were chosen. Cells in which the chromatin material appeared in loops, thus indicating transition stages from pachynema to second contraction and from second contraction to diakinesis, as well as very poorly fixed cells were not included in the tabulation.

TABLE

Number of arms	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Number of nuclei	2	2	3	4	5	4	9	14	10	8	8	2	6	3

It will be noted that the largest number of cells contain over seven arms indicating clearly that there cannot be seven paired chromosomes in *O. Lamarkiana*. In addition to the evidence thus brought forward for the lack of chromosome homology in *Lamarkiana*, it seems to be perfectly clear that fixation techniques used for Œnothera material preserve this period of meiosis very imperfectly. I believe that perfect fixation would show here twelve univalent chromosomes and one pair, the latter being in a true strepsitene condition.

The arms extending from the central mass are interpreted as chromosomes or portions of chromosomes. Later loops appear, FIGS. **39-40.** Rarely the sides of such loops are appressed. In the loop arrangements chromosomes may be joined end to end, but at this stage, FIG. **39**, it is difficult to determine the points of attachment. Sometimes the peripheral portion of the loop is the point of contact and then the two sides will be formed by different chromosomes. In many cases the loop is formed by but a single chromosome, FIG. **40**. In other cases several chromosomes are definitely linked end to end to form a loop, FIG. **41.**

The somatic chromosomes are not linked even in the last somatic division, FIG. **26.** There is no clear evidence that the chromatic threads at the so called resting stage or during leptonema and zygonema are continuous, FIGS. **28-33**. Such a condition cannot be determined when the threads are too delicate to permit of detailed study, or when a coagulum caused by fixation is present to obscure the ends. Some pachytene threads show definite ends, FIGS. **34-35**, and ends are present at the early second contraction period. It is certain, however, that at late second contrac-

tion and at diakinesis the chromosomes become linked in a closed chain, FIGS. **39-43**.

The progress of the formation of the chain of chromosomes in the later phases of second contraction can be followed. At the beginning of the period the threads are separate. Later free ends of arms may be found bent towards one another or in contact Thus in FIG. **37**, the free ends of arms *a* and *b* are bent towards each other so that they nearly touch. At a somewhat later stage loops begin to appear. There is evidence that these are formed by the end to end association of the arms. It seems probable that *x* in FIG. **39** is the point of union of the two arms *a* and *b*, while at *y* the inner ends of chromosomes *b* and *c* have become attached and are in the process of breaking away from the central coagulum. The slight connection between threads *d* and *e* strongly suggests that they may have been formerly in contact but are now drawn apart. If it can be assumed that slight constriction at *z* represents the union of chromosomes *f* and *g* and that each of the other loops or threads represents a chromosome or a portion of one it is possible to count fourteen of these structures in the nucleus. Five of these, *a* to *g* are linked together in a chain. Two others *h* and *n* are linked in a short loop, *k* has a definite free end. The remaining structures are separate and partially obscured in the coagulum. FIG. **39** then represents an intermediate condition between FIGS. **37** and **38**, which show all arms with free ends and FIGS. **42** and **43**, which show twelve chromosomes linked in a closed chain. Thus FIG. **39** gives evidence for the formation of the chain of chromosomes at second contraction, as it supplies not only a step in the transition of the nucleus from the stage of FIGS. **37** and **38** to the stage of FIGS. **40-43**, but also shows stages in the actual behavior of the threads at this period of meiosis.

As condensation proceeds during second contraction the chromosomes become more clearly differentiated since they grow shorter and thicker. Some of them appear on peripheral loops, FIGS. **40-41**, while others are still closely gathered in a central group, FIG. **40**. Those in the central group finally separate and a closed chain of twelve chromosomes, FIGS. **42-43**, emerges from the confusion of second contraction. The two homologous chromosomes form a pair by themselves always apart from the chain of twelve, FIG. **43**.

Throughout the prophases of meiosis in *O. Lamarckiana* there has been no suggestion of pairing of homologous chromosomes except for the

two which emerge in the side-by-side relation and these may fairly be assumed to come from the two paired threads that have been observed in zygonema, pachynema and second contraction, FIGS. **33, 34*m*, 37*m*** and **38*m***. The twelve chromosomes which form the closed chain cannot be considered as closely homologous. By this is meant that none of the twelve have sufficient resemblance in structure to satisfy the conditions of parasynapsis. Why they should be joined so regularly end to end and in an arrangement by which alternate chromosomes probably pass to opposite poles is a most interesting problem of Œnothera cytology.

DISCUSSION.

The study of meiosis in the Œnotherae has long offered some of the most perplexing problems in plant cytology, partly because of difficulties of technique but chiefly for the reason that the forms first studied, *O. Lamarckiana*, *lata*, *rubrinervis*, *gigas*, *biennis*, *rubricalyx*, etc., are impure or heterogametic species in which most of the chromosomes fail to pair after the method of parasynapsis but instead become associated end to end to form one or more closed chains. Through the use of mixtures of acetic acid and alcohol, I have been able to throw some light on the structure of the chromatic thread system during the confusion of the so called stage of synizesis. However, the most significant information on the problem was obtained through a careful comparison of the prophases of *O. Hookeri*, a homozygous species having perfectly pairing chromosomes, with the heterogametic *O. Lamarckiana*, a species in which a closed chain of twelve chromosomes occurs together with an independent pair.

The early stages of meiosis are identical in the two species. Chromatic bodies appear in varying numbers and sizes. Then a very delicate thread system develops, FIGS. **1-3** and **26-28**, which shortly passes into leptonema. In early leptonema a difference may be observed in the two species with respect to the behavior of the fine chromatic threads. Parallel arrangements become evident in *O. Hookeri*, FIGS. **4-5**, while none were observed in *O. Lamarckiana*, FIG. **29**.

The threads now lengthen greatly in each species, FIGS. **6** and **30**, and preparations of the entire nucleus and even sections present a picture of great confusion. The delicate filaments begin to contract and in thin sections of nuclei of *O. Hookeri* parallel threads may be observed,

FIGS. **8-11**, in contrast with the almost complete absence of parallel threads in *O. Lamarkiana*, FIGS. **31-33**. The process of shortening and thickening continues in each species. In *O. Hookeri*, it is accompanied by parallel associations of the delicate filaments constituting a zygonema, while in *O. Lamarckiana* this side-by-side association does not take place, FIGS. **31-33**. At pachynema in *O. Hookeri* it is possible to trace and count the shortened and thickened zygotene threads which are seven in number, FIGS. **12-17**, corresponding to the number of the pairs of chromosomes formed later. *O. Lamarkiana*, by contrast, shows thirteen heavy filaments, twelve of which are univalent, FIGS. **34-35**. Free ends are present in both species, indicating that the spireme is not continuous. The seven filaments present in *O. Hookeri* are frequently split in some degree, demonstrating their bivalent nature. In *O. Lamarckiana*, only one of the thirteen has been observed to be split, this representing the pair of chromosomes which conjugate.

The process of shortening and thickening continues until during the stage of second contraction it is possible to count in *O. Hookeri* seven bivalent arms extending from a chromatic coagulum in the center of the nucleus, FIGS. **18-24**. These arms become free and form the seven pairs of chromosomes clearly shown at diakinesis, FIG. **25**.

Second contraction in *O. Lamarckiana* is so confusing that it is difficult to follow the fate of the thirteen threads. However, thirteen arms have been counted extending from a central coagulum, FIGS. **37-38**, indicating that threads of the previous period have shortened and thickened just as the seven threads have done in *O. Hookeri*. It also appears that twelve of these thirteen arms become joined so that each end of an arm is attached to the end of two other arms, thus forming a closed chain. The remaining bivalent arm becomes the pair of independent chromosomes.

Telosynapsis has been the usual interpretation of chromosome association in the Œnotherae, chiefly because of the presence of chains of chromosomes. However, in *O. Hookeri*, seven pairs of chromosomes occur at diakinesis and I have shown that this peculiarity is represented, in other periods of meiosis, by parallel threads during leptonema and zygonema and by seven bivalent threads during pachynema and second contraction. This is a history characteristic of parasynapsis.

As for the occurrence of telosynapsis in *O. Lamarkiana*, this conclusion has been reached mainly through the study of diakinesis, which stage

cannot furnish conclusive evidence as to the mode of chromosome association since synapsis does not take place at this time. Furthermore it is quite probable, from the work of GELEI, the SCHREINERS, GRÉGOIRE, MC CLUNG, and many others on meiosis, that all cases of telosynapsis are in reality an incorrect interpretation of the parallel threads of leptonema and zygonema which are the most significant stages of parasynapsis. What then is the mode of chromosome association in *O. Lamarckiana?*

It seems best to review very briefly the salient points of telosynapsis to show that even if such a manner of chromosome association might occur, the arrangement in *O. Lamarckiana* does not accord with such a scheme. In reported cases of telosynapsis in plant material (FARMER and MOORE, DIGBY, MOTTIER, SANTOS, etc.) parallel threads have been described during leptonema and zygonema, but interpreted as being due to a lengthwise division in the chromosomes at anaphase or telophase of the last somatic division. During pachynema, homologous chromosomes are said to become associated end to end and then to bend at the point of attachment so they come to lie side-by-side. At diakinesis homologous chromosomes form definite pairs which have a side-by-side relation to one another. I think there can be little doubt that the interpretation of the early parallel threads and the end to end association of chromosomes during pachynema is incorrect, but it is important to note that these accounts of telosynapsis admit a system of parallel threads in both early and late prophase stages and that bivalent chromosomes are formed by the conjugation of two homologous chromosomes.

Such conditions have not been described for *O. Lamarckiana* or any other species of *Œnothera* in which the chromosomes are arranged in chains. Parallel threads have never been observed during early stages of meiosis. From pachynema to diakinesis, regardless of the state of the spireme, all accounts agree that the chromosomes in the chain are separated and distinct from one another and show no evidence of pairing by twos either end to end or side-by-side.

Cytologically, the chromosomes have been designated as non-homologous and this interpretation finds support in breeding experiments (BARTLETT, 1915; BLANCHARD, 1929). This lack of pairing of non homologous chromosomes in *Lamarckiana* distinctly does not conform to accounts of telosynapsis. It is better that the term telosynapsis should be used in its original meaning. The term asynapsis may appropriately be applied

to the condition found in *O. Lamarckiana* where chromosomes give no indication of synapsis.

This phenomenon is not new in the literature. Osawa (1913) has described identical conditions in *Taraxacum platycarpum* and *T. albidum*. In the latter species the embryo develops parthenogenetically. When meiosis in *T. albidum*, is carefully compared with chromosome development in *T. platycarpum*, a species in which seeds develop normally, the same differences appear to exist as have been described as occuring between *O. Hookeri* and *O. Lamarckiana*. No cases of parallel threads were observed in *T. albidum*, while they do occur in *T. platycarpum*. The chromosomes of *T. albidum* are described as being linked at diakinesis like a » string of pearls «. This stage in *T. platycarpum* shows the usual paired arrangement of its chromosomes.

Håkansson (1925) reports a somewhat similar condition in the genus, *Godetia*. In the two species *G. amoena* and *G. Whitneyi* the chromosomes pair normally at diakinesis, showing no tendency to form chains. However, in the hybrid form *G. amoena* × *G. Whitneyi*, chains of chromosomes are present at diakinesis. At metaphase and sometimes in late diakinesis the chromosomes separate from one another and lie free in the nucleus, the number of univalents and bivalents varying. This failure of the chromosome chains to remain intact throughout the metaphase accounts for the Mendelian ratios reported by Rasmusson (1921) for this cross.

The failure of chromosomes to pair has also been described by Rosenberg (1917) for pathenogenetic Hieracia. Asynapsis is known to occur in numerous cases of hybridization (Rosenberg, 1917; Federley, 1913; Sax, 1922; Täckholm, 1922, etc.). Usually the species in which asynapsis is present are sterile or when able to reproduce do so through some anomaly of meiosis or reproduction as in parthenogenesis (Owasa, 1913; Rosenberg, 1917, 1926, 1927); the doubling of chromosomes to form tetraploids (Winge, 1917; Clausen and Goodspeed, 1925; Rosenberg, 1926; Karpechenko, 1927). budding from the nucellus (Täckholm, 1922); univalents acting as a group while bivalents divide as usual at the heterotypic anaphase (Täckholm, 1922); maternal and paternal chromosomes acting as groups (Goodspeed and Clausen, 1917a, b and c). It is probable that nearly all cases of apomixis will show asynapsis.

In the Œnotherae possessing a chain of chromosomes the sterility

and failure of the chromosomes to pair is similar to the conditions existing in the forms mentioned above. These facts together with much of the breeding data make it very probable that these species of *Œnothera* are of a hybrid nature. The anomaly of meiosis through which they are able to reproduce themselves is due to the factor which causes maternal and paternel chromosomes to remain as two groups that segregate as groups at the heterotypic metaphase.

The conclusions from the cytological peculiarities of the two types of meiosis illustrated by *O. Hookeri* and *O. Lamarckiana* find support from the genetical behavior of these two species and of other Oenotherae resembling them in the arrangement of the chromosomes at diakinesis.

The breeding behavior of *O. Lamarkiana* and other species containing a closed chain of chromosomes such as *O. muricata*, *O. biennis*, etc., are too well known for a detailed account in this paper. SHULL (1928, p. 98) has listed the peculiarities shown by these species, as follows : a) » the true-breeding of demonstrably heterozygous parents; b) the formation of » twin hybrids « in the F1 of certain species crosses; c) the production of relatively rare segregations in the F2 and later generations from crosses; d) the occurrence of unlike reciprocal hybrids; e) the relative rarity of occurrence of inheritance ratios closely simulating the typical Mendelian ratios; f) the occurrence of large degrees of pollen-ovule and seed-sterility; and the g) ability of practically every pair of species within the subgenus *Onagra*, however divergent in phenotypic characteristic, to cooperate in the production of fertile hybrids «. To this list may be added the presence of only one or two unusually large linkage groups. These peculiarities are possible on the assumption that the maternal and paternal chromosomes alternate one with another in the chains and pass as groups to opposite poles at the heterotypic anaphase. The analyses of BARTLETT, (1915, 1916), RENNER (1917), COBB and BARTLETT (1919) and LEHMANN (1922) are in accord with this assumption.

In *O. Hookeri* and other species having wholly paired chromosomes, the breeding behavior as well as the development of the chromosomes is very different from the species containing the closed chains. There are, so far as is known, only three natural species having all paired chromosomes, *O. grandiflora* (material of DAVIS), *O. Hookeri* and certain material of the related species *O. franciscana*. *O. desserens* and *O. blandina* are homozygous mutants from *O. Lamarckiana* and possess seven paired chromosomes.

O. flava has seven pairs of chromosomes and arose as one of a set of twin hybrids from the cross *O. suaveolens* × *O. strigosa.*

O. flava is an F 1 hybrid from the cross *O. suaveolens* × *O. strigosa.* As its chromosomes are not linked, independent segregation should take place. That it actually does is shown by Oehlkers' (1926) results, which give fair Mendelian ratios considering the small numbers in the cultures.

	Spotted	Not spotted	Ratio
1919	40	12	3.33 : 1
1920	27	8	3.40 : 1
1922	77	21	3.66 : 1
	144	41	3.46 : 1

	Pollen fertile	Pollen sterile	Ratio
1919	37	15	2.5 : 1
1920	26	9	3.0 : 1
1922	80	18	4.4 : 1
	143	42	3.4 : 1

	Normal	Weak	Ratio
1919	52	9	5.8 : 1
1920	35	10	3.5 : 1
1922	86	21	4.1 : 1
	173	40	4.4 : 1

It should also be noted that the percentage of seedlings that do not develop because of whitish or yellow cotyledons is very suggestive of the monohybrid ratio :

1919	21.2 %
1920	23.7 %
1922	22.1 %
	22.3 %

Due to the large number of undeveloped plants Oehlkers does not consider that the independent segregation of chromosomes is responsible for these ratios. However, if the lethal gene or genes were not linked with the genes governing the characters in question, these characters would not be affected by incomplete germination or weak plants and Mendelian ratios would be expected. Furthermore it is not probable that ratios so close to those expected from Mendelian behavior would occur in three successive generations on the same four characters unless some mathematical system were present.

Oehlkers further divides the progeny of *O. flava* into thirteen classes on the appearance of the plant as a whole, which indicates that the chromosomes, though sufficiently homologous to pair, still must differ in many genes and that these chromosomes then segregate independently. It is usually not possible to obtain significant genetical ratios from the study of the general appearance of the plant form. If the individual characters had been more carefully analyzed and followed throughout the whole history of the cross more ratios indicating Mendelian behavior would probably have been detected.

The other twin hybrid, *O. ablata*, developed from the cross *O. suaveolens* × *O. strigosa*, is a form which has a closed chain of chromosomes and breeds true. This is just what would be expected, as in this case independent segregation of the chromosomes does not take place. At reduction division, the maternal chromosomes pass to one pole and the paternal to the other. In fertilization only the paternal and maternal groups unite to form *O. ablata*.

It appears then that as far as is known only the species of *Œnothera* with paired chromosomes show a breeding behavior that is in full accord with that expected of forms in which there exists independent segregation of chromosomes. It is the Œenotherae which contain a chain of chromosomes at diakinesis which show the breeding peculiarities so characteristic of the group.

Mendelian inheritance has been reported in *O. Lamarckiana*, but it is the independent pair of chromosomes that makes this possible. De Vries (1901, 1903, 1913) and Davis (1918, 1921) have shown that *O. brevistylis* segregates close to a simple 3 : 1 ratio from crosses with *O. Lamarckiana*, and Davis (1926) gives similar data for the segregation of a brevistylis form of *O. nanella* from crosses with *O. nanella*. Shull (1926) reports Mendelian segregation for *O. Lamarckiana mut. vetaurea* from *O. Lamarckiana*. As the *vetaurea* gene present in this form proved to be independent of the *brevistylis* factor, Shull believes O. *vetaurea* to be a marker for a third linkage group, and suggests that the chromosomes configuration at diakinesis will be a closed chain of ten and two homologous pairs. Cobb and Bartlett (1919), Cobb (1921) and Blanchard (1929) have reported certain Mendelian ratios in *O. pratincola*. Further cases of Mendelian segregation are known in other forms and are probably to be explained by the presence of independent pairs of homologous chromosomes.

The two types of breeding behavior in the species of Œenotherae seemed to be the result of such differences in meiosis and chromosome segregation as are reported in this comparison of *O. Hookeri* with *O. Lamarckiana*.

SUMMARY

1. The premeiotic stages in the archesporial cells of *O. Hookeri* and *O. Lamarckiana* are similar. Chromatic bodies which vary in number from one to twenty appear after the last somatic mitosis. These disappear with the development of a delicate thread system which fills the nucleus. Beginning with the prophase stages of meiosis the two species present different histories in the development of the chromosomes.

2. In early leptonema the delicate threads of the earlier stage thicken sufficiently so that they may be traced fort short distances. *O. Hookeri* shows many of these threads parallel and occasionally two threads may be observed emerging from the same chromatic granule. Except for one observed case of parallelism, the threads in *O. Lamarckiana* are never found to be parallel. This case of parallelism probably represents the two homologous chromosomes which conjugate in this species. In neither species do the threads seem to form a reticulum. The filaments lengthen greatly so that later stages of leptonema are marked by a confusing system of chromatic threads, which nearly fills the nucleus.

3. After fixation in acetic-alcohol, the coagulum and the great contraction described by Œnothera cytologists as synizesis is not present. There is some contraction but in place of the coagulum there is present a definite system of threads winding within the nucleus. In thin sections of such nuclei the threads are found to be parallel in *O. Hookeri*, constituting a zygonema, but parallelism is absent in material of *O. Lamarckiana*.

4. The zygotene threads of *O. Hookeri* shorten and thicken so that during pachynema they may be traced and counted. They are seven in number. Some of them are definitely split, indicating that they have been formed by the side-by-side association of the parallel filaments of earlier stages. In *O. Lamarkiana* on the contrary, thirteen threads may by counted during pachynema, twelve of which are univalent and one a zygotene bivalent.

5. These threads continue to shorten and thicken so that at second contraction they may be seen as short arms radiating from a central

coagulum. At this period the arms are seven in number in *O. Hookeri* and thirteen in *O. Lamarckiana.* In the former species they are all definitely bivalent, while only one is bivalent in *O. Lamarckiana.*

6. Through the continued condensation of these arms the seven bivalent chromosomes of *O. Hookeri* are formed. The twelve univalent arms in *O. Lamarckiana* unite end to end to form the closed chain of twelve non-homologous chromosomes. The single bivalent arm in this species forms the one pair of homologous chromosomes, which lies apart from the closed chain of twelve.

7. The history of the prophase in *O. Hookeri* indicates that the chromosomes become associated side-by-side after the parasynaptic interpretation of synapsis.

8. The apparent absence of pairing among the twelve non-homologous chromosomes of *O. Lamarckiana* does not support the telosynaptic interpretation of synapsis, for telosynapsis postulates the end to end pairing of homologous chromosomes, although they later become associated side-by-side. The development and association of the twelve non-homologous chrosomes to form a chain in the prophase stages of meiosis in *O. Lamarckiana* is better described by the term asynapsis.

LITERATURE CITED

1915 *Bartlett, H. H.* : Mass mutation in *Œnothera pratincola;* Bot. Gaz., LX, 423-456.

1916 *Id.* : The status of the mutation theory, with especial reference to *Œnothera;* Am. Nat,, L, 513-529.

1883 *Beneden, E. (van)* : Recherches sur la maturation de l'œuf et la fécondation; Arch. de Biol., IV, 265 640.

1929 *Blanchard F. C* : The genetical constitutions of *Œnothera pratincola* and its revolute-leaved mutations; Journ. Wash. Acad. Sci., XIX, 115-125.

1924 *Boedijn, K.* : Die typische und heterotypische Kernteilung der *Œnothera;* Zeitschr. f. Zellen- u. Gewebel., I, 265-277.

1925 *Id.* : Der Zusammenhang zwischen den Chromosomen und Mutationen bei *Œnothera Lamarckiana.* Amsterdam, J. H. Bussy.

1926 *Carothers, E. E.* : The maturation divisions in relation to the segregation of homologous chromosomes; Quart. Biol., I, 419-435.

1925 *Clausen, R. E. and Goodspeed, T. H.* : Interspecific hybridzation in *Nicotiana* II. A tetraploid *glutinosa-tabacum* hybrid, an experimental verification of WINGE's hypothesis; Genetics, X, 278-284.

1922 *Cleland, R. E.* : Reduction divisions in the pollen mother cells of *Œnothera franciscana;* Amer. Jour. Bot., IX, 391-413.

1923 *Id.* : Chromosome arrangements during meiosis in certain Œnotheras; Amer. Nat., LVII, 562-566.

1924 *Id* : Meiosis in the pollen mother cells of *Œnothera franciscana sulfurea;* Bot. Gaz., LXXVII, 149-170.

1926a *Id.* : Meiosis in the pollen mother cells of *Œnothera biennis* and *Œnothera biennis sulfurea;* Genetics, XI, 127-162.

1926b *Id.* : Cytological study of meiosis in anthers of *Œnothera muricata;* Bot. Gaz., LXXXII, 55-70.

1927 *Id.* : The genetics of *Œnothera* in relation to chromosome behavior, with special reference to certain hybrids; Verhand. des V. Internat. Kong. f. Vererbungs., Berlin, 1927.

1921 *Cobb, F.* : A case of Mendelian inheritance complicated by heterogametism and mutation in *Œnothera pratincola;* Genetics, VI, 1-42.

1919 *Cobb, F. and Bartlett, H. H.* : On Mendelian inheritance in crosses between mass-mutating and non-mass-mutating strains of *Œnothera pratincola;* Journ. Wash. Acad. Sci., IX, 462-483.

1929 *Darlington, C. D.*: Ring-formation in *Œnothera* and other genera: Jour. Genetics, XIX, 345-364.

1909 *Davis, B. M.*: Cytological studies on *Œnothera;* I. Pollen development of *Œnothera grandiflora;* Ann Bot., XXIII, 551-571.

1910 *Id.*: Cytological studies on *Œnothera;* II. The reduction divisions of *Œnothera biennis;* Ann. Bot., XXIV, 631-651.

1911 *Id.*: Cytological studies on *Œnothera;* III. A comparison of reduction divisions of *Œnothera Lamarckiana* and *Œnothera gigas;* Ann. Bot., XXV, 941-974.

1918 *Id.*: The segregation of *Œnothera brevistylis* from crosses with *Œnothera Lamarckiana;* Genetics, III, 501-533.

1921 *Id.*: Malnutrition as a cause of irregularities in the segregation of *Œnothera brevistylis* from crosses with *Œnothera Lamarckiana;* Genetics, VI, 574-586.

1926 *Id.*: The segregation of *Œnothera nanella brevistylis* from crosses with *nanella* and with *Lamarckiana;* Genetics, XI, 57-72.

1924 *Emerson, S. H.*: The absence of chromosome pairing during meiosis in *Œnothera biennis;* Papers Mich. Acad. Sci. Arts and Letters, IV, 111-114.

1905 *Farmer and Moore*: On the meiotic phase (reduction division) in animals and plants; Quart. Jour. Mic. Sci., XLVIII, 489-557.

1913 *Federley, H.*: Das Verhalten der Chromosomen bei der Spermatogenese der Schmetterlinge *Pygaera anachoreta, curtula* und *pigra* sowie einiger ihrer Bastarde. Ein Beitrag zur Frage der konstanten intermediären Artbastarde und der Spermatogenese der Lepidopteren; Zeit. Ind. Abs. u. Vererb., IX, 1-110.

1907 *Gates, R. R.*: Pollen development in hybrids of *Œnothera lata* and *O. Lamarckiana* and its relation to mutation; Bot. Gaz., XLIII, 81-115.

1907 *Geerts, J. M.*: Ueber die Zahl der Chromosomen von *Œnothera Lamarckiana;* Ber. d. deutsch. Bot. Gesellsch., XXV, 191-195.

1917a *Goodspeed, T. H., and Clausen, N. E.*: The nature of the F 1 species hybrids between *Nicotiana sylvestris* and varieties of *Nicotiana tabacum,* with special reference to the conception of reaction system contrasts in heredity; Univ. Calif. Publ. Bot., V, 301-346.

1917b and c *Id.*: Mendelian factor differences versus reaction system contrasts in heredity I, II; Am. Nat., LI, 31-46.

1925 *Håkansson, A.*: Zur Zytologie der Gattung *Godetia;* Hereditas, VI, 258-274.

1926 *Id.*: Ueber das Verhalten der Chromosomen bei der heterotypischen Teilung schwedischer *Œnothera Lamarckiana* und einiger ihrer Mutanten und Bastarde; Hereditas, VIII, 255-304.

1928 *Id.*: Die Reduktionsteilung in den Samenanlagen einiger Œnotheren; Hereditas, XI, 129-181.

1927 *Karpechenko, G. D.* : The production of polyploid gametes in hybrids; Hereditas, IX, 349-368.

1927 *Kihara, Hitashi* : Ueber das Verhalten der « end to end » gebundenen Chromosomen von *Rumex acetosella* und *Œnothera biennis* während der heterotypischen Kernteilung. Beitrag zur Frage der Para- und metasyndese; Jahrb. Wiss. Bot., LXVIII, 429-460.

1929 *Kulkarni, Chandrakant, G.* : Meiosis in pollen mother cells of strains of *Œnothera pratincola* Bartlett; Bot. Gaz., LXXXVII, 218-259.

1922 *Lehmann, Ernst* : Die Theorien der Œnotheraforschung. Jena, Gustav Fischer, P. 526.

1928 *Leliveld, J. A.* : Some remarks on the cytology of *Œnothera;* Rec. Trav. Bot. Neer., XXVa, 237-243.

1927 *Mc Clung, C. E.* : Synapsis and related phenomena in *Mecostethus;* Jour. Morph. and Phys., XLIII, 181-252.

1928 *Id.* : The generic constancy of a particular chromosome in *Mecostethus gracilis, lineatus* and *grossus;* Arch. de Biol., XXXVIII, 503-529.

1926 *Morgan, T. H.* : The theory of the gene; Yale University Press, New Haven, p. 343.

1926 *Oehlkers, F.* : Erblichkeit und Zytologie einiger Kreuzungen mit *Œnothera strigosa;* Jahrb. Wiss. Bot., LXV, 401-446.

1913 *Osawa, J.* : Studies on the cytology of some species of *Taraxacum;* Arch. f. Zellf., X, 450-469.

1921 *Rasmusson, H.* : Beiträge zu einer genetischen Analyse zweier *Godetia*-Arten und ihrer Bastarde; Hereditas, II, 144-289.

1917 *Renner, O.* : Die tauben Samen der Œnotheren; Ber. d. deutsch. Bot. Gesellsch., XXXIV, 858-869.

1917 *Rosenberg, O.* : Die Reductionsteilung und ihre Degeneration in *Hieracium;* Svensk. Bot. Tidskr., XI, 145-206.

1926 *Id.* : Ueber die Verdoppelung der Chromosomenzahl nach Bastardierung; Ber. deut. Bot. Gesellsch., XLIV, 455-460.

1926-27 *Id.* : Die semiheterotypische Teilung und ihre Bedeutung für die Entstehung verdoppelter Chromosomenzahlen; Hereditas, VIII, 305-338.

1922 *Sax, K.* : Sterility in wheat hybrids. II. Chromosome behavior in partially steril hybrids; Genetics, VII, 513-552.

1926 *Schwemmle, J.* : Vergleichend zytologische Untersuchungen an Onagraceen. II. Die Reduktionsteilung von *Eucharidium concinnum;* Jahrb. Wiss. Bot., LXV, 778-818.

1927 *Id.* : Der Bastard *Œnothera berteriana* × *Onagra (muricata)* und seine Zytologie; Jahr. Wiss. Bot., LXVI,579-595.

1920 *Sharp, L. W.* : Somatic chromosomes in *Tradescantia;* Amer. Jour. Bot., VII, 341-354.

1927 *Sheffield, F. M. L.* : Cytological studies of certain meiotic stages in *Œnothera;* Am. Bot., XLI, 779-816.

1914 *Shull, G. H.* : A peculiar negative correlation in Œnothera hybrids; Jour. Gen., IV, 83-102.

1926 *Id.* : « Old Gold » flower color, the second case of independent inheritance in *Œnothera*; Genetics, XI, 201-239.

1928 *Id.* : Œnothera cytology in relation to Genetics; Am. Nat., LXII, 97-114.

1927 *Sinotô, Y.* : Microsporogenesis in *Œnothera sinuata* L.; Tokyo. Bot. Mag., 225-234.

1910 *Stomps, T. J.* : Kernteilung und Synapsis bei *Spinacia oleracea;* Biol. Centralbl, XXXI, 257-320.

1888 *Strasburger, E.* : Ueber Kern- und Zellteilung im Pflanzenreich, nebst einem Anhang über Befruchtung; Hist. Beitr., I.

1922 *Täckholm, C.* : Zytologische Studien über die Gattung *Rosa*; Acta Horti Bergiani, VII, 97-381.

1922 *Taylor, W. R.* : Organization of heterotypic chromosomes; Sci., LVI, 635.

1926 *Valcanover, R.* : Contribution à l'étude de la réduction dans l'*Œnothera biennis;* La Cellule, XXXVII, 203-222.

1901-1903 *de Vries, Hugo* : Die Mutationstheorie (2 vols). Leipzig : Veit & Cº.

1913 *Id.* : Gruppenweise Artbildung. Berlin, Gebruder Borntraeger.

1925 *Wilson, E. B.* : The cell in development and heredity. New-York, Macmillan. Third edition.

1917 *Winge, O.* : The chromosomes, their numbers and general importance; Compt. rend. trav. Lab. Carlb., XIII, 131-275.

DESCRIPTION OF FIGURES

All figures were sketched with the aid of a camera lucida under the Zeiss *apochromatic objective 1,5 mm. (num. aper 1,30) in combination with the compensating ocular 20 ×, giving a magnification of 2400 diameters.*

Figs. 1-25, Œnothera Hookeri.

FIG. **1**. Nucleus immediately during the last somatic division in the archesporium. The chromosomes are present as slightly bent rods. Tellyesniczky, section 10 μ.

FIG. **2**. Stage following that shown in fig. **1**. Some of the chromosomes have fragmented so that seventeen bodies may be counted. Delicate threads are forming. Tellyesniczky, 10 μ.

FIG. **3**. The chromatic bodies have almost disappeared and a fine chromatic thread system has developed. Acetic-alcohol, 1 : 2, 10 μ.

FIG. **4**. Early leptonema. The threads are thicker and individual filaments may be traced for short distances. Many of them are parallel and a number of these end in chromatic bodies. Tellyesniczky, 13 μ.

FIG. **5**. Similiar to fig. **4**, but fixed in acetic-alcohol, 1 : 3. The chromatic bodies are not so numerous, 10 μ.

FIG. **6**. Late leptonema. The threads are longer and they now wind about within the nucleus in a confused ball. Tellyesniczky, 10 μ.

FIG. **7**. The stage generally described as synizesis, conspicuous after killing in aqueous solutions and believed by the author to express imperfect fixation. The threads are much contracted and closely gathered in a knot. Strong Flemming, 13 μ.

FIG. **8**. Section of nucleus in zygonema. At *a* two threads may be observed winding about each other, while *b* is split in the middle and *c* and *d* are double at one end. Acetic-alcohol, 1 : 3, 3 μ.

FIG. **9**. Section of another nucleus in zygonema. Acetic-alcohol, 1 : 3, 3 *u*.

FIG. **10**. Similar to fig. **9**, but the threads are thicker. Picric acid in 95 % alcohol, acetic acid, formol, 15 : 5 : 1, 3 μ.

FIG. **11**. Optical section of a nucleus in zygonema. The confusion existing when such a large number of filaments are present is great, but some parallel threads may be seen. Acetic-alcohol, 1 : 3, 10 μ.

FIG. **12**. Pachynema. Seven threads may be traced in the nucleus. One of these has a free end, and another *b*, is split. Tellyesniczky, 15 μ.

FIG. **13**. Similar to fig. **12**. One thread, *a*, has a free end, *b* and *c* are split and *d* is short and thick with a free split end. Tellyesniczky, 15 μ.

FIG. **14.** Similar to FIG. **12.** LINDSAY JOHNSON, 15 μ.

FIG. **15.** The seven threads of FIG. **14** isolated and drawn in détail.

FIG. **16.** Similar to FIG. **12.** TELLYESNICZKY, 15 μ.

FIG. **17.** The seven threads of FIG. **16** isolated and drawn in detail.

FIG. **18.** Second contraction. Seven arms radiate from a central coagulum, six of them are split. LINDSAY JOHNSON, 15 μ.

FIG. **19.** Second contration. The coagulum has separated into two parts. One arm lies free in the nucleus and is split. LINDSAY JOHNSON, 15 μ.

FIG. **20.** Second contraction. Similar to FIG. **19,** one arm free and its two parts recognizable as chromosomes. TELLYESNICZKY, 15 μ.

FIG. **21.** Second contraction. One arm showing no split has separated from the central coagulum. Six arms are still attached. LINDSAY JOHNSON, 15 μ.

FIG. **22.** Second contraction. Three arms have become detached from the mass, one of which shows a split. LINDSAY JOHNSON, 15 μ.

FIG. **23.** Second contraction. Three arms have become separated, one is definitely recognisable as a condensed bivalent chromosome in the form characteristic of diakinesis, while the other two show a split condition. LINDSAY JOHNSON, 15 μ.

FIG. **24.** Late second contraction. Seven pairs of chromosomes of which six are closely grouped. LINDSAY JOHNSON, 15 μ.

FIG. **25.** Diakinesis. Seven pairs of chromosomes. TELLYESNICZKY, 15 μ.

Figs. 26-43, Œnothera Lamarckiana.

FIG. **26.** Chromosomes of *O. Lamarckiana* during the last somatic division in the archesporium. Acetic-alcohol, 1 : 2, 10 μ.

FIG. **27.** Chromatic bodies. Acetic-alcohol, 1 : 2, 10 μ.

FIG. **28.** Thread system. Acetic-alcohol, 1 : 2, 10 μ.

FIG. **29.** Early leptonema. The threads are not parallel and they are apparently not in the form of a reticulum. Acetic-alcohol, 1 : 3, 10 μ.

FIG. **30.** Late leptonema. The chromatic threads are long and delicate, winding in a confused ball within the nucleus. Acetic-alcohol, 1 : 3, 10 μ.

FIG. **31.** Optical section through an entire nucleus at the time when zygonema would be evident if this stage were present in *O. Lamarckiana*. On the contrary the threads are single. Acetic-alcohol, 1 : 3, 15 μ.

FIG. **32.** Thin section of nucleus in the same stage shown in FIG. **31.** All threads are single. Acetic-alcohol, 1 : 3, 3 μ.

FIG. **33.** Stage similar to FIG. **32.** All threads but two are single. These show one of the two cases of parallelisms observed at this stage. Acetic-alcohol, 1 : 3, 3 μ.

FIG. **34.** Pachynema. Thirteen threads are present, *a* probably represents the pair of bivalent chromosomes, *b* is short and thick suggesting the arms which appear in the following stage, *c* has one free end. TELLYESNICZKY, 15 μ.

FIG. **35** Pachynema. Similar to FIG. **34,** but showing more filaments with free ends. TELLYESNICZKY. 15 μ.

FIG. **36.** Second contraction. An irregular mass of chromatic material. LINDSAY JOHNSON, 15 μ.

FIG. **37.** Second contraction. Thirteen arms extend from a central coagulum; *a* to *l* are single; *m* shows a split at its distal end. TELLYESNICZKY, 15 μ.

FIG. **38.** Second contraction. Similar to FIG. **37** TELLYESNICZKY, 15 μ.

FIG. **39.** Second contraction. Thirteen loops or arms are shown; *a* and *b* have joined end to end at *x*, *b* and *c* at *y*, *g* and *f* at *z*. *d* and *e* are connected by a thread. TELLYESNICZKY, 15 μ.

FIG. **40.** Late second contraction. Chromosomes may now be distinguished. TELLYESNICZKY. 15 μ.

FIG. **41.** Late second contraction. Some chromosomes have been thrown out into a large loop, others are arranged in a smaller one, while the remainder twist about in a compact knot TELLYESNICZKY, 15 μ.

FIG. **42.** Diakinesis. The closed chain of twelve chromosomes is shown. TELLYESNICZKY, 15 μ.

FIG. **43.** Diakinesis. The pair of homologous chromosomes is shown together with the closed chain. TELLYESNICZKY, 15 μ.

CONTENTS

PAGES

Introduction 271

Material and methods 275

DESCRIPTION OF MEIOTIC PROPHASES IN *Œnothera Hookeri* 276

A) Chromatic bodies 276

B) Delicate thread system 277

C) Leptonema 277

D) Synizesis 279

E) Zygonema 281

F) Pachynema 282

G) Second contraction 283

DESCRIPTION OF THE MEIOTIC PROPHASES IN *Œnothera Lamarckiana* 284

A) Chromatic bodies 284

B) Delicate thread system 284

C) Leptonema 284

D) Synizesis 285

E) Zygonema 286

F) Pachynema 286

G) Second contraction 287

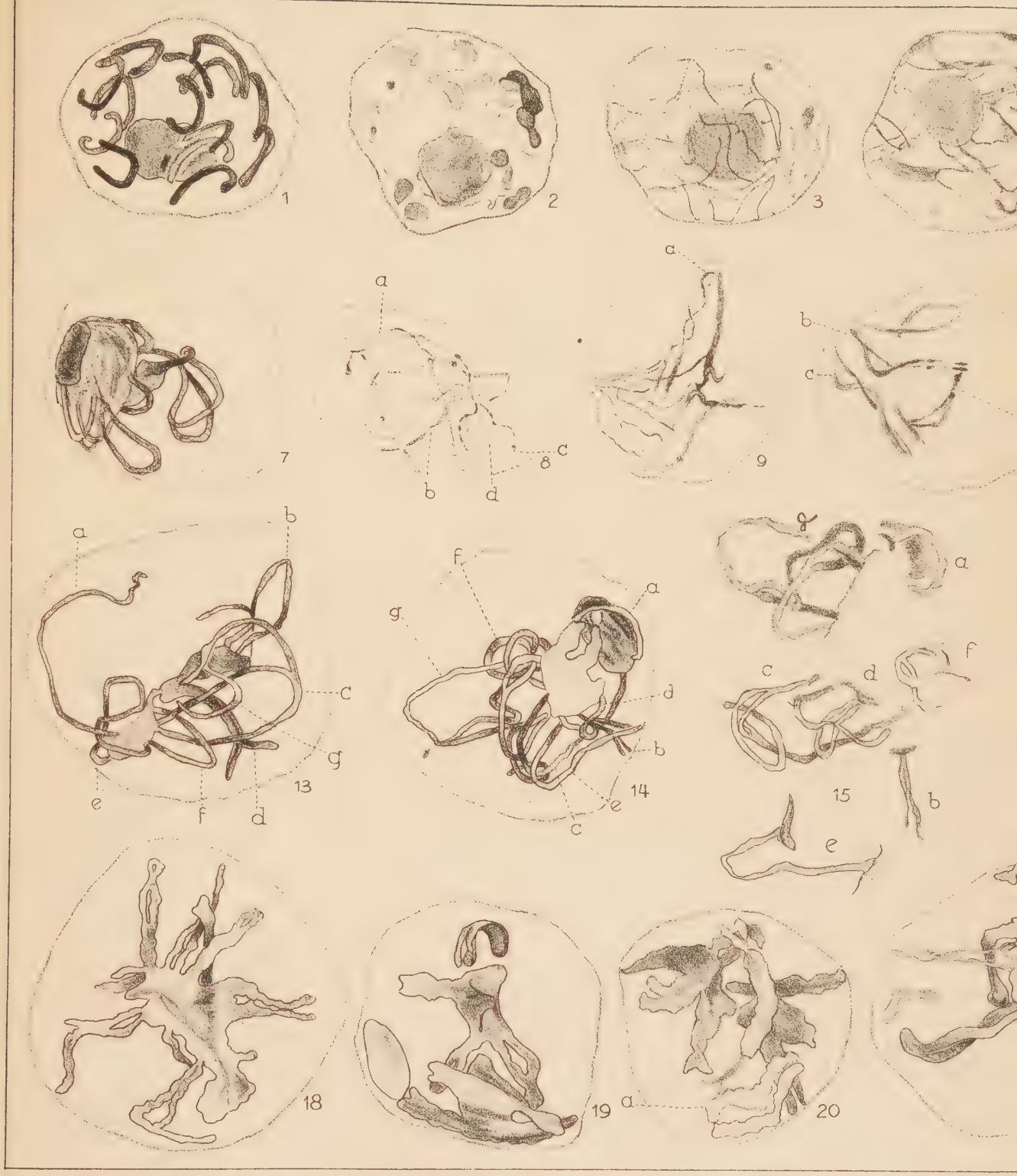
Discussion 290

Summary 297

Literature cited 299

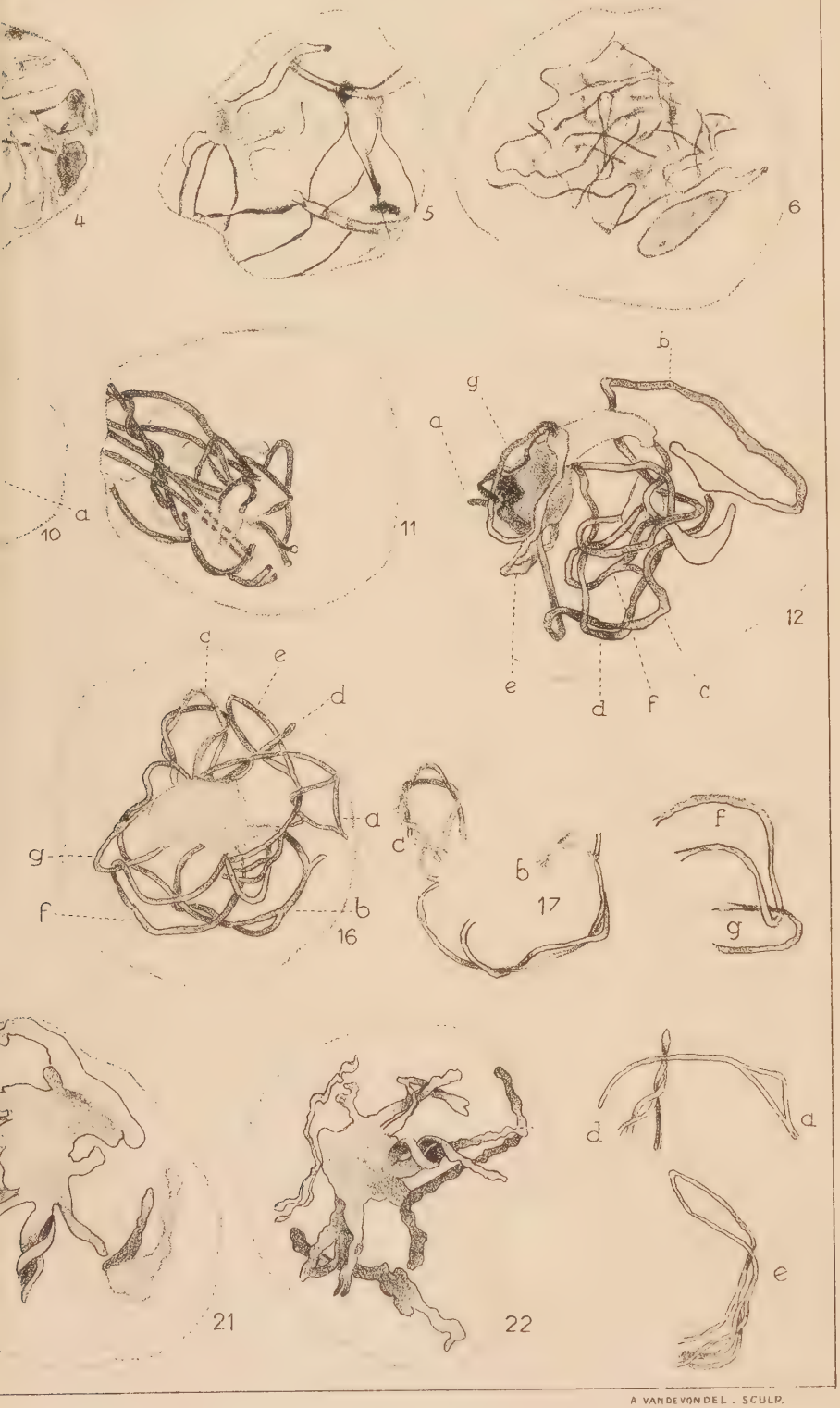
Description of figures 303

Plate I



T.E.WEIER AD NAT.DEL

LITH. J. MARCHAL. BRUX.



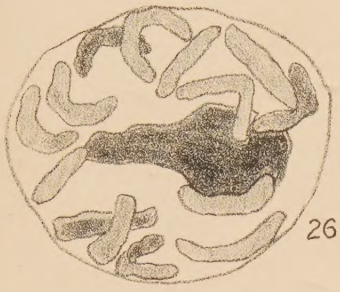
A VANDEVONDEL . SCULP.

Plate II

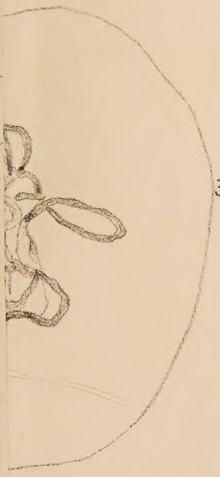
T.E.WEIER AD NAT. DEL.

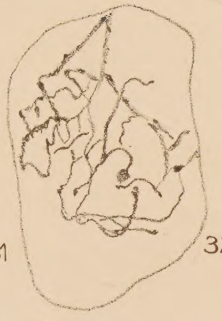
IMP. J. MARCHAL. BRUX.

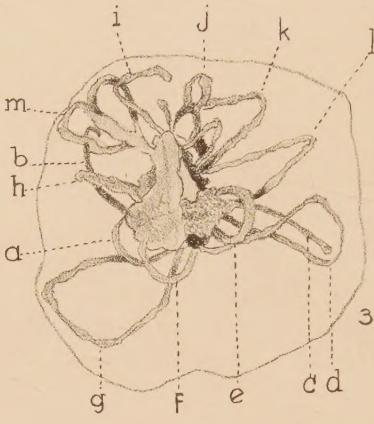
25


26

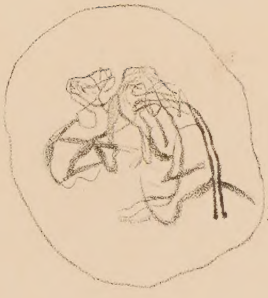
27

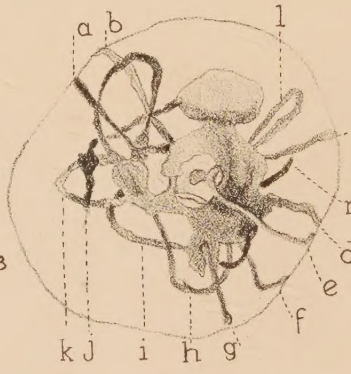

31


32

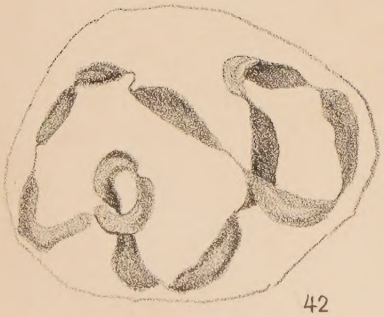


34


33



35


42

43

Ant. Vandevondel .sculp.